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Variation in phenology and overall performance traits can help to explain the plant invasion process amongst Mediterranean ecosystems

Irene Martín-Forés[1,2*], Miguel A. Casado[2], Isabel Castro[3], Alejandro del Pozo[4], Marco A. Molina-Montenegro[5,6], José M. de Miguel[2], Belén Acosta-Gallo[2]

1 *Department of Biogeography and Global Change, National Museum of Natural Sciences, Spanish National Research Council (MNCN-CSIC), C/ José Gutierrez Abascal 2, 28006, Madrid, Spain* **2** *Ecology, Department of Biodiversity, Ecology and Evolution, Complutense University of Madrid, C/ José Antonio Nováis 2, 28040, Madrid, Spain* **3** *Department of Ecology, Autonomous University of Madrid, C/ Darwin 2, Ciudad Universitaria de Cantoblanco, 28049, Madrid, Spain* **4** *Centro de Mejoramiento Genético y Genómica Vegetal, Facultad de Ciencias Agrarias, Universidad de Talca, Avda. Lircay s/n, Talca, Chile* **5** *Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad Católica del Norte, Coquimbo, Chile* **6** *Centro de Ecología Molecular y Funcional, Universidad de Talca, Avda. Lircay s/n, Talca, Chile*

Corresponding author: *Irene Martín-Forés* (imfores@mncn.csic.es)

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Abstract

Plant traits such as phenological development, growth rate, stress tolerance and seeds production may play an important role in the process of acclimatisation to new environments for introduced plants. Experiments that distinguish phenotypic plasticity from ecotypic differentiation would allow an understanding of the role of plant traits in the invasion process. We quantified the variation in phenological and overall performance traits associated with the invasion process for three herbaceous species native to Spain and invasive to Chile (*Trifolium glomeratum*, *Hypochaeris glabra* and *Leontodon saxatilis*). We grew plants from native and exotic populations along rainfall gradients in outdoor common gardens, located in the native and the introduced ranges and measured plant survival, phenology (days to flowering), biomass and seed output. Days to flowering was positively correlated with precipitation of the origin population for *T. glomeratum* and the native populations of *H. glabra*, but this pattern was not adaptive, as it was not associated with an increase in performance traits of these species. Phenology may instead reflect ecotypic differentiation to the environmental conditions of the original populations. Comparison between ranges (i.e. performance in both common gardens) was only possible for *L. saxatilis*. This species showed little

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variation in phenology and both native and exotic populations had higher fitness in the introduced range. This suggests that plasticity enhances invasiveness through increased propagule pressure in the novel environment. Our findings highlight the utility of common garden experiments in examining patterns of phenological and performance traits that relate to species invasiveness.

Keywords

Asteraceae, biological invasions, biomass, common garden, *Hypochaeris glabra*, invasiveness, *Leontodon saxatilis*, phenology, precipitation, range expansion, seed output, survival, *Trifolium glomeratum*

Introduction

Despite recently gaining attention and considerable resources having been invested into studying habitat invasibility and species invasiveness (Richardson and Pyšek 2006, Guo et al. 2015), understanding the role played by invasive plant traits in the process of acclimatisation to the novel conditions along the introduced range still remains a key knowledge gap in invasion biology (but see MacDougall and Turkington 2005, Molina-Montenegro et al. 2010, Moravcová et al. 2015). Some overall performance traits have been suggested to be crucial for plant invasiveness, such as plant growth rate, environmental tolerance, phenological development and seed production (Noble 1989, Pyšek and Richardson 2007, van Kleunen et al. 2010, Moravcová et al. 2015). In this sense, it has been shown that greater plant growth and seed output account for the invasiveness of many alien plant species (Grotkopp and Rejmánek 2007), where species producing a greater number of seeds increase their propagule pressure and hence, their chances for establishment. However, the role of plant phenology in biological invasion processes and species invasiveness has often been neglected despite considerable differences in phenological development between native and invasive species having already been pointed out (Wolkovich and Cleland 2011, Godoy and Levine 2014).

Plant invasiveness often involves rapid adaptive evolution and/or genetic drift. Thus, invasive plants often undergo phenotypic differentiation to cope with novel environments through a combination of two processes, phenotypic plasticity and ecotypic differentiation (Maron et al. 2004, 2007, Molina-Montenegro et al. 2013). Phenotypic plasticity is the ability of a plant genotype to modify its physiology/morphology in response to environmental conditions and has been indicated as a mechanism that can mediate the establishment and dispersal in the new area (Valladares et al. 2005, 2006, Rejmánek et al. 2005, Richards et al. 2006, Pyšek and Richardson 2007, Pichancourt and van Klinken 2012). However, plasticity is not necessarily adaptive (i.e. does not always improve fitness) and the role that it plays in invasion processes remains still unclear (but see Chambel et al. 2005). Ecotypic differentiation may occur for the invasive plant species in the introduced range through selection of the optimal phenotype that provides local adaptation in different geographic locations, leading to many genotypes adapting to particular environmental conditions and thus allowing increased fitness (Lande 2009, Molina-Montenegro et al. 2013, 2018a, Martín-Forés et al. 2017c, 2018). For example, in more humid environments, plant phenology can

show a delay which *a priori* gives plants more time to invest in biomass production and display more dispersal units (Pérez-Ramos et al. 2010).

It is known that these two processes can occur very quickly for annual Mediterranean species (Cocks et al. 1982, Small and Lefkovich 1986, del Pozo et al. 2000) that have been expanded beyond their initial distribution centre. As a result, some functional traits are expected to be affected and result in enhanced environmental tolerance and/or up-take of resources (Molina-Montenegro et al. 2018b).

Mediterranean-type ecosystems worldwide are considered as biodiversity hotspots and therefore targets for conservation policies (Myers et al. 2000), but despite many conservation efforts, the frequency and intensity of biological invasions in Mediterranean ecosystems is still considerable (Arianoutsou et al. 2013, Martín-Forés et al. 2017a). In this sense, the Mediterranean climate-type region of central Chile constitutes an interesting natural lab for exploring variations in functional traits caused by these mechanisms. Associated with the Spanish conquest that took place in the 16th century, many exotic species were accidentally introduced into Chile (Martín-Forés et al. 2012, 2017a) and became naturalised in the Mediterranean climate region of central Chile.

Previous studies centred in the Mediterranean-type region of central Chile have shown a combination of these mechanisms for some species. For instance, for the invasive Asteraceae *Taraxacum officinale*, both plasticity and ecotypic differentiation for various traits were found in relation to latitudinal (Molina-Montenegro and Naya 2012, Molina-Montenegro et al. 2013, 2018a) or altitudinal (Molina-Montenegro et al. 2012) gradients in Chile. Additionally, ecotypic differentiation along environmental gradients has been observed for phenological development of *Medicago polymorpha* in Chile (del Pozo et al. 2000, 2002a, 2002b). In relation to performance traits, two of the most common invasive species in Chile, the Asteraceae *Leontodon saxatilis* subsp. *rothii* and *Hypochaeris glabra* showed increased propagule pressure and longer distance dispersal for exotic populations and at the introduced range (Martín-Forés et al. 2017c, Martín-Forés et al. 2018).

In particular, this study focuses on three annual species that are native to Spain and invasive to Chile, being broadly distributed in both the native and the introduced ranges, far beyond the Mediterranean climate distribution (Martín-Forés et al. 2012, Casado et al. 2015, 2018; See Suppl. material 1: Figure S1 for detailed information). Here, we bring together and compare plasticity and ecotypic differentiation not only on performance traits but also on phenology of two representatives of the Asteraceae family, *Leontodon saxatilis* subsp. *rothii* and *Hypochaeris glabra* (Martín-Forés et al. 2017, Martín-Forés et al. 2018) and one of the Fabaceae family, *Trifolium glomeratum* that has been selected because of its importance as a fodder plant.

Since the introduction of these three species into Chile (according to the first record, no more than 120 years ago; Castro et al. 2005), they have encountered different abiotic and biotic conditions in the introduced range from those of their native range (i.e. edaphic and climate characteristics, photoperiod, land use patterns, livestock grazing) as well as community interactions such as competence, tolerance and facilitation

processes (Martín-Forés et al. 2015, 2016, 2017b). Accordingly, studies carried out in both the native and the introduced range of a species have been highlighted as of especial importance because they constitute the most direct test of determinants of invasiveness (Williams et al. 2008, van Kleunen et al. 2010). Thus, the aim of this study was to compare variations in phenology and performance traits associated with the invasion process of *L. saxatilis*, *H. glabra* and *T. glomeratum* into Chile. We used seeds from five Spanish populations and five Chilean populations collected along rainfall gradients in both countries and we evaluated all the populations in two common gardens located in Madrid, Spain and Cauquenes, Chile, that is in the native and introduced range, respectively. We explored *i)* whether the geographic origin of the plant collections (hereafter populations) could explain differences in plant phenology and performance traits within the same common garden trial and *ii)* whether individuals of the three species responded through phenotypic plasticity to the different climatic conditions existing in the two common garden trials regardless their population. The native populations of the three species have been longer exposed to local environmental conditions in the native range than exotic populations in the introduced one; therefore they have had more time to develop local adaptation through ecotypic differentiation. Thus, we would expect Spanish populations to present greater ecotypic differentiation than Chilean ones; if so, the delay in phenology while increasing the amount of precipitation on the origin population would be stronger for Spanish populations. Likewise, if the delay in phenology turns out to be adaptive, plants will display greater biomass and seed output.

Methods

Study area

The study was conducted in grasslands of the Mediterranean regions of Spain and central Chile (typically called *dehesas* and *espinales*, respectively) used for extensive livestock grazing, especially sheep and cattle. These grasslands present slightly acidic soils and are adapted to Mediterranean-type climate, characterised by having scarce precipitation in summer (drought period from June to September in the Northern hemisphere and from December to February in the Southern hemisphere).

For the three species, we selected five Spanish native populations and five Chilean exotic populations representative of the rainfall gradient existing in the Mediterranean regions of both countries. In Chile, the five populations were located in the central region (from 32°31' to 37°00'S and 70°46' to 72°34'W), with mean annual precipitation ranging from 300 to 1200 mm (Table 1; Suppl. material 2: Figure S2). In Spain, the five populations were located in the centre-west of the Iberian Peninsula (from 38°16' to 39°33'N and from 5°23' to 6°20'W), with mean annual precipitation ranging from 450 to 950 mm (Table 1; Suppl. material 2: Figure S2). The total annual precipitation (mm), mean annual temperature (°C) and number of months with drought period or

Table 1. Geographic and climatic characteristics of the populations of *Hypochaeris glabra*, *Trifolium glomeratum* and *Leontodon saxatilis*. TMED is mean annual temperature; P is the annual precipitation and MWD is the number of months with drought period or water deficit per year.

Country	Site	Code	Species collected	Latitude	Longitude	TMED (ºC)	P (mm)	MWD
Chile	Runge	Ch1a	*T. glomeratum*	33°00'25"S	70°53'45"W	14.27	303	8
Chile	Catapilco	Ch1b	*H. glabra*	32°35'53"S	71°18'50"W	16.19	352	8
Chile	Melipilla	Ch2a	*H. glabra, T. glomeratum*	33°49'18"S	71°18'58"W	17.00	412	8
Chile	Pumanque	Ch2b	*L. saxatilis*	34°37'48"S	71°42'54"W	15.01	719	5
Chile	Boldo	Ch3	*H. glabra, T. glomeratum, L. saxatilis*	35°58'52"S	72°13'38"W	14.33	794	5
Chile	Quirihue	Ch4	*H. glabra, T. glomeratum, L. saxatilis*	36°15'20"S	72°32'58"W	13.14	972	5
Chile	Yumbel	Ch5	*H. glabra, T. glomeratum, L. saxatilis*	37°00'26"S	72°34'01"W	13.33	1168	4
Spain	Castuera	S1	*H. glabra, T. glomeratum, L. saxatilis*	38°46'20"N	5°34'48"W	16.89	468	4
Spain	Fuente de Canto	S2	*H. glabra, T. glomeratum, L. saxatilis*	38°16'33"N	6°20'22"W	15.81	572	4
Spain	Madroñera	S3	*H. glabra, T. glomeratum, L. saxatilis*	39°25'23"N	5°47'48"W	15.42	666	4
Spain	Ibor	S4	*H. glabra, T. glomeratum, L. saxatilis*	39°32'53"N	5°22'57"W	14.46	859	4
Spain	Logrosán	S5	*H. glabra, T. glomeratum, L. saxatilis*	39°21'28"N	5°25'04"W	16.17	913	3

water deficit per year, an index calculated as the number of months in which monthly mean temperature is at least double the monthly precipitation, were determined for each population (Table 1). Climate variables were obtained from WorldClim (Hijmans et al. 2005), at a resolution of 30 arc-seconds.

Selected populations ideally contained the three species studied. Flower heads of *L. saxatilis*, *H. glabra* and *T. glomeratum* were collected from the five native (i.e. Spanish) and the five exotic (i.e. Chilean) populations in spring of 2010, at the end of flowering periods for most plants (i.e. May-June in Spain and October-November in Chile). Mature flower heads were randomly collected from 50 individuals of each species at each population; the distance between the individuals selected within each population was at least 1 m from each other and they were haphazardly distributed around an area of approximately one hectare (for detailed information about data collection for *L. saxatilis* and *H. glabra*, see Martín-Forés et al. 2017c, 2018, respectively).

Common garden growing conditions

Seeds from the 50 collected flower heads were pooled together. In each range, seeds randomly chosen from each population were germinated in petri dishes on to filter paper and irrigated every two days with 5 ml of distilled water. In the case of *L. saxatilis* and *H. glabra*, peripheral fruits and unbaked fruits were respectively chosen for subsequent planting because of their greater success in pre-germination studies (see Martín-Forés et al. 2017c, 2018 for detailed information). In the case of *T. glomeratum*, seeds were previously scarified by immersing them in boiling water for 5 minutes; afterwards, they were inoculated with *Rhizobium trifolii* before transplanting the seedlings to the common garden to ensure nodulation and nitrogen fixation.

When the radicles of plants (F_2) reached 5 mm, seedlings were transplanted into subplots within two common garden trials, one located at the Faculty of Agronomy of the Polytechnic University of Madrid, Spain (40°26'N, 3°44'W; 600 m a.s.l.; 15 °C mean annual temperature; 484 mm mean annual precipitation) in the native range and the other one located in central Chile, at the Experimental Centre of Cauquenes-INIA, Chile (35°58'S, 72°17'W; 140 m a.s.l.; 14.4 °C; 748 mm mean annual precipitation), in the introduced range. The experiments were set outdoors under semi-controlled conditions where large herbivores were excluded. Planting was conducted directly in the soil when the rain period started, i.e. in June 2012 in Chile and October 2012 in Spain. For each species in the Spanish trial, 20 seedlings of each population were planted in subplots of 200 x 50 cm after removing surface vegetation through ploughing; however, due to space limitations, in the Chilean trial, only ten seedlings of each population were planted and the subplots size was 100 × 50 cm. In both countries, the distance between plants was 20 cm and the separation between neighbouring subplots was 30 cm. A complete randomised design was used with three replicated subplots per population. Thus, there was a total of 87 subplots within each site: 45 containing populations from Spain (three species × five populations × three replicates) and 42 containing populations from Chile (three species x five populations (four in the case of *L. saxatilis*) x three replicates). The total number of individuals planted in Chile was 870 and in Spain was 1740. The non-targeted surface vegetation was continuously removed over the experimental period by hand to ensure plants in both common gardens experienced similar levels of competition. No additional treatment, such as fertilisation, occurred in any of the common gardens.

Functional traits

The experiment lasted for 180 and 250 days at the Chilean and Spanish common gardens, respectively. At each common garden, weekly values of precipitation and daily values of mean temperature were obtained from the meteorological stations that were located closest to the experiments (i.e. Cauquenes INIA meteorological station: 35°57'S, 72°17'W; 164 m a.s.l. in Chile and Madrid Ciudad Universitaria meteorological station: 40°27'N, 3°43'W; 640 m a.s.l. in Spain; see graphs in Fig. 1 and the Suppl. material 3: Figure S3 for detailed meteorological data).

Plant survival and phenology were recorded three times a week from sowing to flowering and every two days from flowering to plant fructification. Plants that died prior to accomplishing fruit maturity were no longer employed for assessing performance traits, while plants that accomplished maturity were considered dead after reaching 75% senescence. Phenological observation included the date when each individual got the first floral bud and was used to calculate the days from planting to flowering.

The number of flower heads per plant was counted for every individual. Flower heads were collected after they had produced fruits but before the infructescence opened, to ensure we captured all seeds and avoided propagules spreading. The average number of fruits per flower head was calculated for each individual by averaging the number of

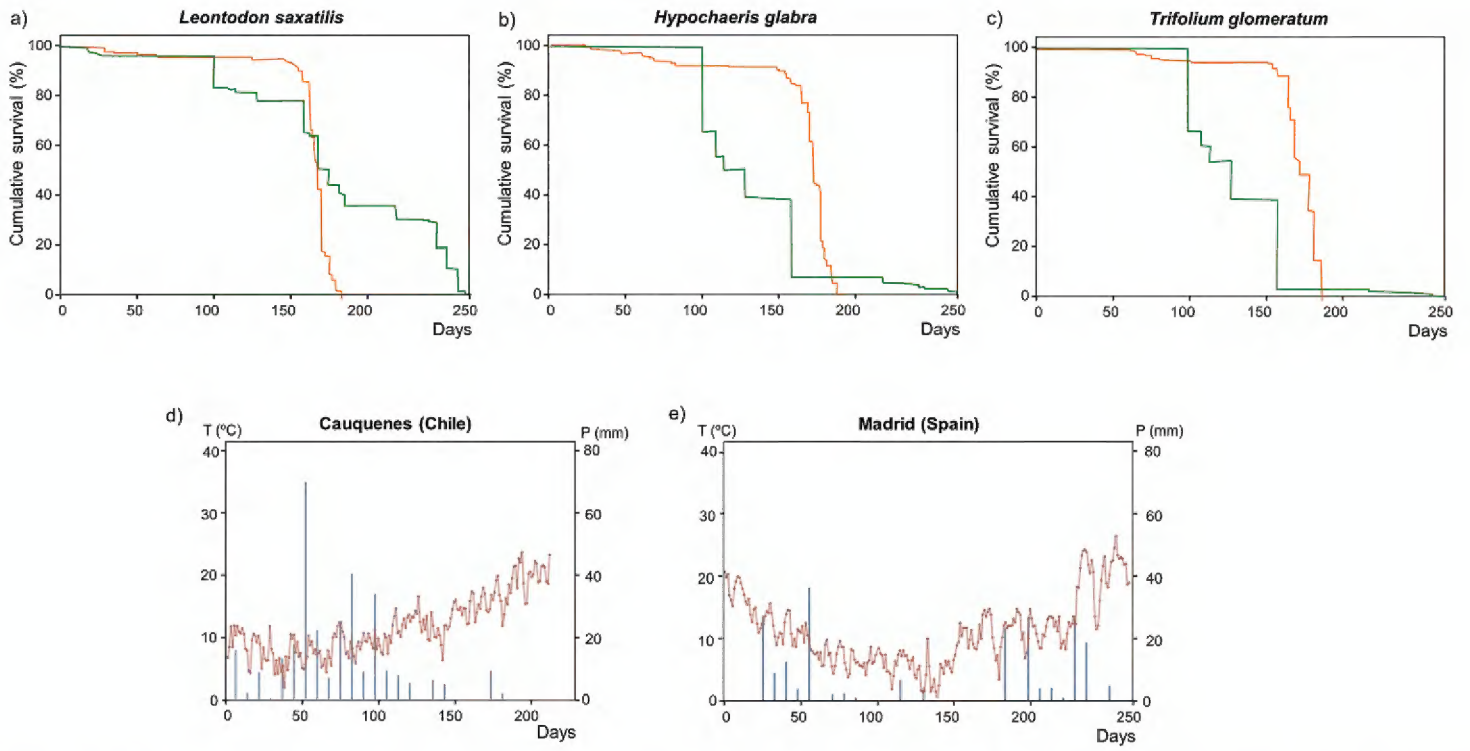

Figure 1. Kaplan-Meier survival curves for *Leontodon saxatilis* (**a**), *Hypochaeris glabra* (**b**) and *Trifolium glomeratum* (**c**) in trials at both the native (green line) and the introduced ranges (orange line). Daily medium temperature values (°C) during the experiment are shown with a continuous brown line, while precipitation (mm/week) is represented by blue bars for both the common garden at the introduced range (**d**) and the common garden at the native range (**e**).

fruits counted over five flower heads that were collected from each plant when it reached around 50% senescence. The total seed output per plant was estimated by multiplying the average number of fruits per flower head by the number of flower heads per plant.

Once each individual had reached around 75% senescence, plants were harvested. Flower heads were removed and then the vegetative part was oven-dried at 60 °C for 72 hours. Afterwards, aboveground dry biomass (hereafter biomass) was weighed.

Due to the high mortality rate of *H. glabra* and *T. glomeratum* in the Spanish trial, further comparisons of phenology and performance traits between ranges (common gardens) were only possible to assess for *L. saxatilis*.

Data analyses

All analyses were performed in R v 3.2.3 (R Core Team 2015). To check differences in survival rates associated with climatic conditions of both common gardens, the cumulative survivals of the three species, expressed by their Kaplan-Meier curves, were plotted taking into consideration the environmental conditions of each common garden. For each species, comparisons for populations of both countries of origins (Spanish vs. Chilean) between Kaplan-Meier curves from the time seedlings were sown were performed with the R package survival (Therneau 2015).

We used mixed effects models using the base stats package plus lme4 (Bates et al. 2014) to explore differences in phenological and performance traits of *L. saxatilis*, *H. glabra* and

T. glomeratum associated with the country of origin of the populations. We considered the plant individual as the unit of analysis (*L. saxatilis*: n = 340; *H. glabra*: n = 186; *T. glomeratum*: n = 268). Models were fitted taking into account phenology (i.e. days to flowering), plant growth (i.e. dry aboveground biomass) and estimated seed output per plant as response variables. We used mixed effects models with a Gaussian error distribution for the three response variables. Fixed effects included the country of origin (Spain and Chile) and the precipitation on the population (as populations were selected along a rainfall gradient) for *H. glabra* and *T. glomeratum*. In the case of *L. saxatilis*, we also explored whether phenology and performance traits of this species varied between common gardens located in the native and in the introduced ranges; thus not only the previous fixed factors but also the range where the common garden was emplaced were included. The subplot where populations were planted in the common garden was included as the random effect nested within population. All the possible models, including origin and precipitation (and range in the case of *L. saxatilis*) as predictors (as well as their interactions), were computed.

We compared the possible models differing in the structure of fixed effects fitted by maximum likelihood. We calculated the Akaike Information Criterion corrected for small sample size (AICc). We selected the best-fit models (lowest AICc presenting differences in their AICc lower than 2; Burnham and Anderson 2002) employing the AICcmodavg package (Mazerolle 2015). The parsimony principle was applied on the subset of best models based on AICc and the model with the lowest number of parameters was chosen for subsequent analyses (Cox et al. 2006). Selected models were fitted by Restricted Maximum Likelihood and significant values for fixed effects were calculated with a type-III ANOVA analysis with the lmerTest package (Kuznetsova 2017). Model validation of the best-fit model was based on visually assessing the normality of residuals. To test over-dispersion, we checked that the residual deviance was lower than the residual degrees of freedom (Zuur et al. 2009).

In order to evaluate whether a delay in phenological development could entail an increase in plant performance, we also performed mixed-effects models for performance traits (biomass and seed output) in which we entered days to flowering as predictor, precipitation as co-variable and subplot where populations were planted in the common garden nested within the population as random effects. These models were performed by splitting the plant individuals by origin (i.e. Spanish and Chilean). Marginal r coefficients of these relationships as well as of the relationships between precipitation and phenology and performance traits were obtained per country of origin employing the R package MuMIn (Barton 2018). Finally, outliers that exceeded three times the interquartile range were removed prior to analyses, which only occurred for 1.5% of cases.

Results

There were differences between the climatic conditions of both Mediterranean regions; rainfall gradient was broader and number of months with water deficit longer in Chile than in Spain (300–1200 mm vs. 450–950 mm and 4–8 months vs. 3–4 months, respectively; Table 1).

The cumulative survivals of the three species, expressed by their Kapplan-Meier curves, were clearly different at both ranges, being significantly lower in the native range (Spanish trial) than in the introduced range (Chilean trial) (Fig. 1a–c, Suppl. material 4: Figure S4). In the Spanish trial, *H. glabra* and *T. glomeratum* – and, to a lesser extent also *L. saxatilis* – showed an abrupt mortality after 100 days from planting, whereas in the Chilean trial, the cumulative survival remained high (around 90%) until the end of the experiment. The high mortality in the native range could be related to the scarce precipitation during late autumn and winter (from 1 December to 22 March; see Fig. 1d–e and Suppl. material 3: Figure S3). Due to the high mortality of *H. glabra* (84%) and *T. glomeratum* (94%) in the Spanish common garden, the comparison of phenology and performance traits between ranges (common gardens) was only possible for *L. saxatilis*.

According to the generalised linear mixed-effects models, the factors that explained most of the variation of phenology and performance traits for different populations varied amongst species (Table 2). For *T. glomeratum*, both origin of and precipitation on the population had a significant effect on days to flowering, that being the phenological development was significantly longer for Spanish populations than for Chilean ones (days to flowering for Spanish populations: 142 ± 3; days to flowering for Chilean populations: 131 ± 3). The relationship between days to flowering and the precipitation on the population were significant, regardless of the country of ori-

Table 2. Model coefficients (and Wald-chi square) for the selection of linear models after applying the parsimony criterion on the subset of best models based on AICc, regarding the effects of the country of origin, annual precipitation on the populations (Precip) and range of the common garden on *Leontodon saxatilis*, *Hypochaeris glabra* and *Trifolium glomeratum* traits: days to flowering, biomass and estimated total seed output. Subplot nested within population was considered as random factor in every model. All were fitted to a Gaussian distribution. First factor level: Chile; second factor level: Spain.

	L. saxatilis			*H. glabra*			*T. glomeratum*		
	Days to flowering	**Biomass**	**Seed Output**	**Days to flowering**	**Biomass**	**Seed Output**	**Days to flowering**	**Biomass**	**Seed Output**
Intercept	106.50	56.45	13867.45	115.9	19.18	7522.9	116.5	8.78	5568.4
	(42.20***)	(218.09***)	(16.35***)	(2038.6***)	(83.3***)	(37.6***)	(738.2***)	(109.7***)	(46.1***)
Origin	-1.77	–	12518.95	8.73	10.39	6262.4	11.7	2.78	3285.1
	(0.01)	–	(6.79**)	(5.4*)	(10.6**)	(11.5***)	(18.4***)	(5.4*)	(7.7**)
Precip	0.00	-0.04	-4.41	0.38	–	–	0.02	–	–
	(0.07)	(65.90***)	(1.44)	(0.03)	–	–	(13.6***)	–	–
Range	124.91	-48.86	-11406.30	–	–	–	–	–	–
	(244.74***)	(107.38***)	(11.20***)	–	–	–	–	–	–
Origin*Precip	0.01	–	-13.51	14.10	–	–	–	–	–
	(0.18)	–	(5.52*)	(9.2**)	–	–	–	–	–
Origin*Range	-75.57	–	-10587.77	–	–	–	–	–	–
	(43.45***)	–	(4.85*)	–	–	–	–	–	–
Precip*Range	-0.06	0.03	6.51	–	–	–	–	–	–
	(56.55***)	(38.01***)	(3.10)	–	–	–	–	–	–
Origin*Precip*	0.07	–	11.25	–	–	–	–	–	–
Range	(26.38***)	–	(3.71)	–	–	–	–	–	–

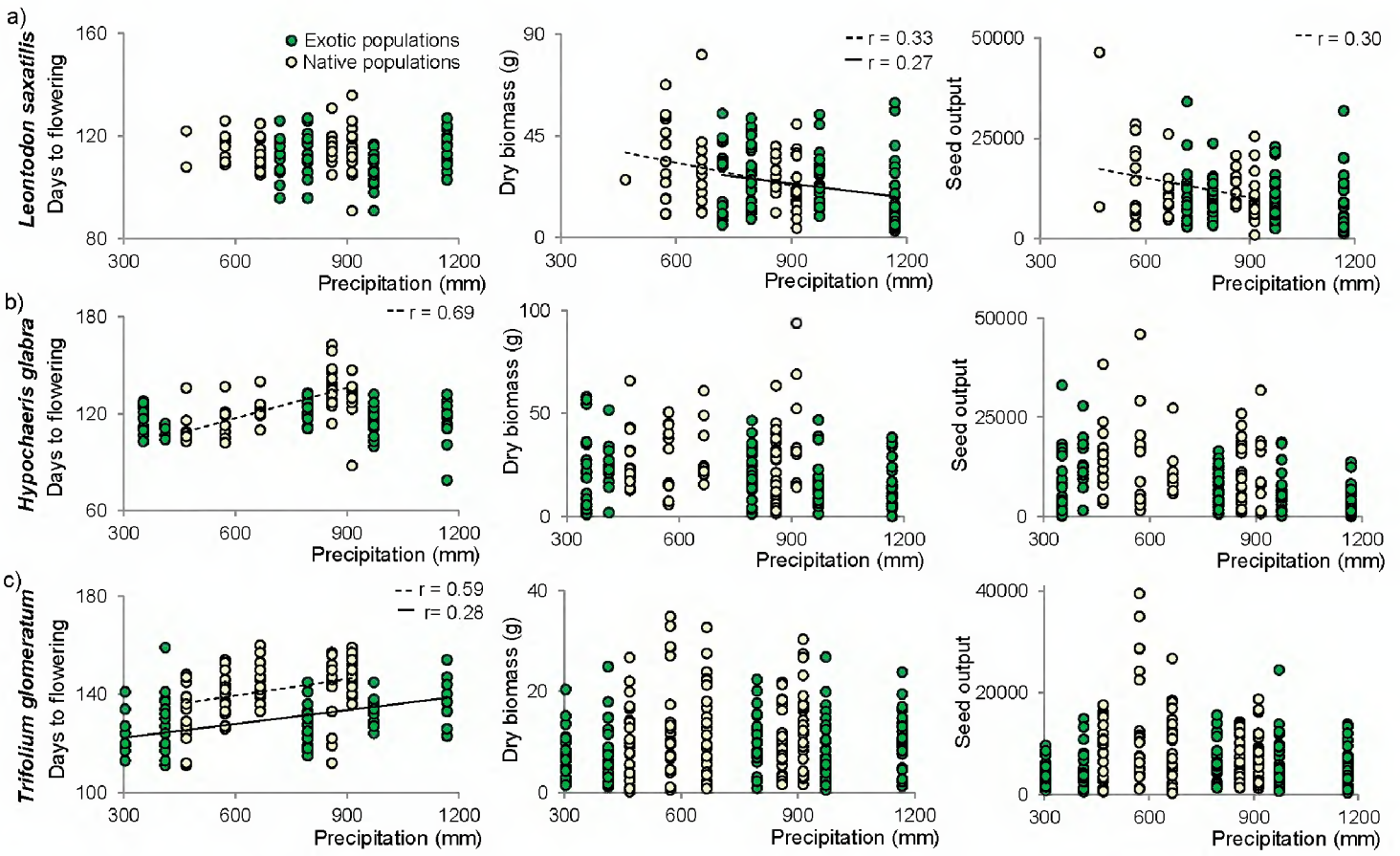

Figure 2. Relationships between annual precipitation on the populations and plant traits (days to flowering, aboveground dry vegetative biomass and seed output per plant) for *Leontodon saxatilis* (**a**), *Hypochaeris glabra* (**b**) and *Trifolium glomeratum* (**c**) evaluated in common garden conditions at the introduced range. Significant relationships are shown by discontinuous (Chilean populations) or continuous (Spanish populations) lines. More detailed results about performance traits of *L. saxatilis* and *H. glabra* are available in Martín-Forés et al. (2017c, 2018).

gin (Spanish populations: r = 0.53; P < 0.05; Chilean populations: r = 0.28; P < 0.05; Fig. 2) In the case of *H. glabra*, the country of origin and its interaction with precipitation had an effect on the days to flowering; there was a close and positive relationship between days to flowering and the precipitation on the population for the Spanish populations (r = 0.69; P < 0.05) but not for the Chilean ones (Table 2; Fig. 2). For *T. glomeratum* and *H. glabra*, differences in days to flowering between the most precocious populations (from the driest provenances) and the latest flowering ones (from the wetter provenances) were up to 27 days. For *L. saxatilis*, the interaction between range and origin (model coefficient for the interaction origin(Spanish)*range(native): t = -6.59; p < 0.001) had a significant influence on phenology (i.e. days to flowering) in the native range, while the effect of precipitation on the population origin was only significant for Spanish populations grown in the native range (model coefficient for the interaction origin(Spanish)*precipitation*range(native): t = 5.14; p < 0.001; Table 2; Fig. 2). Contrary to what was expected, no significant relationships were found between days to flowering and both biomass and seed output (P > 0.05) for any species considered, indicating that a longer time for development does not involve greater reproductive effort.

For *T. glomeratum* and *H. glabra*, the biomass was only determined by the country of origin, with significantly larger plants coming from native populations (*T. glomeratum*:

Spanish populations: 11.8 g ± 0.8 g; Chilean populations: 8.7 g ± 0.5 g; *H. glabra*: Spanish populations: 33.3 g ± 4.2 g; Chilean populations: 19.5 g ± 1.8 g; Table 2; Fig. 2). However, for *L. saxatilis*, there was a negative relationship between biomass and precipitation regardless of the origin of the populations considered (Fig. 2).

Seed output displayed by *T. glomeratum* and *H. glabra* was only determined by the country of origin, with native populations displaying greater number of seeds (*T. glomeratum*: Spanish populations: 8978 ± 1106; Chilean populations: 5525 ± 320; *H. glabra*: Seed output: Spanish populations: 14686 ± 2142; Chilean populations: 7500 ± 1545; Table 2; Fig. 2). For *L. saxatilis*, there was a negative relationship between seed output of native populations and precipitation on the population (Fig. 2).

Common garden comparisons showed that all the studied parameters were mainly influenced by range. Hence, phenology was significantly shorter in the introduced range than in the native one; while biomass and seed output were significantly greater in the introduced range than in the native one (Fig. 3).

Discussion

The need to carry out comparative studies of native *versus* introduced populations in order to detect key aspects to explain the invasion success as those related with functional traits of invaders has been highlighted in the scientific literature (Bossdorf et al. 2005, Molina-Montenegro et al. 2010, 2011, Lemoine et al. 2016). In this sense, our study highlights the differences existing in performance traits and especially in plant phenology associated with the invasion process of three herbaceous plants native to Spain but invasive to Chile.

However, comparison between native and introduced ranges was only possible for *L. saxatilis* due to the high mortality of *H. glabra* and *T. glomeratum* in the Spanish common garden. The three species presented a similar survival curve in the introduced range, where the weather conditions during the common garden experiment were milder and more benign. In this sense, the high survival rate showed by *L. saxatilis* in the native range, regardless of the extreme weather conditions during the Spanish common garden experiment and its resilience after a major drought event (see Fig. 1) could itself constitute an indicator of the plasticity of this species. However, please note that our results regarding phenotypic plasticity should be carefully interpreted as we could not account for genetic distances between mother sources and inter-population gene flow.

The phenology of *L. saxatilis* was mainly influenced by range instead of by country of origin of the populations; thus days to flowering showed different responses for the same population (either native or exotic ones) under different environmental conditions (native vs. introduced range). The variation in *L. saxatilis* phenology between ranges reflects its great capacity to acclimatise to changing environmental conditions (Geng et al. 2007, Gratani 2014). The delay in time to flowering of both Chilean and Spanish populations in the native range (Spain) can be attributed to the lower temper-

atures in autumn and spring and lower precipitation compared to the introduced range (Chile) (Fig. 1 and Suppl. material 3: Figure S3). It is known that higher temperatures (Bradley et al. 1999) and longer day length accelerates plant development in temperate species (Molina-Montenegro and Naya 2012) and differences in day length and night length become more extreme at higher latitude (Bradshaw and Holzapfel 2008). Thus, in Madrid (latitude 40°26'N), the day length or photoperiod is shorter in autumn and winter, but longer in spring and summer than in Cauquenes (latitude 35°58'S). These patterns in temperature and photoperiod gave rise to large differences in the length of the growing season observed between the native and the introduced range.

Changes in flowering phenology amongst different populations constitute an indicator of ecotypic differentiation to the environmental conditions of the provenances where populations originated. According to our findings, populations of *T. glomeratum* and *H. glabra* have mainly undergone variation in their phenology to acclimatise to the new environmental conditions. These species exhibited clear differences in their phenology associated with the country of origin of the populations. In the case of *T. glomeratum*, phenological development was shorter for populations (both native and exotic ones) originating in drier provenances and phenology became lengthened for populations originating in more humid provenances (Table 2; Fig. 3). In fact, similar results were reported by del Pozo et al. (2000, 2002a, 2002b) in another Fabaceae, *Medicago polymorpha*. Regarding *H. glabra*, a similar delay was observed in phenological development for Spanish populations originating in more humid provenances, but this trend was not observed for Chilean populations. The fact that exotic populations of *T. glomeratum* originating in more humid provenances showed a phenological delay in relation to those originating in drier provenances (although this was not shown for exotic populations of the two daisies) could be related with the time since introduction of the three invasive species in central Chile. The leguminous *M. polymorpha* and *T. glomeratum* were first recorded before 1799 and in 1897, respectively (Castro et al. 2005), so they had been naturalised in the introduced range for several decades, possibly with enough time to undergo acclimatisation. Following the same criteria, *H. glabra*, a species that was first recorded in Chile in 1905 (Fuentes et al. 2013), showed differences between native and exotic populations; nevertheless, Chilean populations did not show ecotypic differences amongst them. In contrast, *L. saxatilis* was first recorded in Chile in 1963, therefore it has had only a short time to undergo rapid evolution (Buswell et al. 2011) or to develop further strategies, relying mainly in plastic responses in its phenology and performance traits. However, the significant interactions between range, country of origin and precipitation found in *L. saxatilis* point to ecotypic differences for Spanish populations grown in the native range, where populations from drier provenances have shortened their period of phenological development.

In any case, contrary to what might be expected, the delay in phenology associated with the precipitation on the population showed by *T. glomeratum* and by the native populations of *H. glabra* was not adaptive *sensu stricto* as it did not increase the performance traits of these species. Therefore, this mechanism could allow populations to acclimatise to a wider environmental range (i.e. enhance their invasiveness via increas-

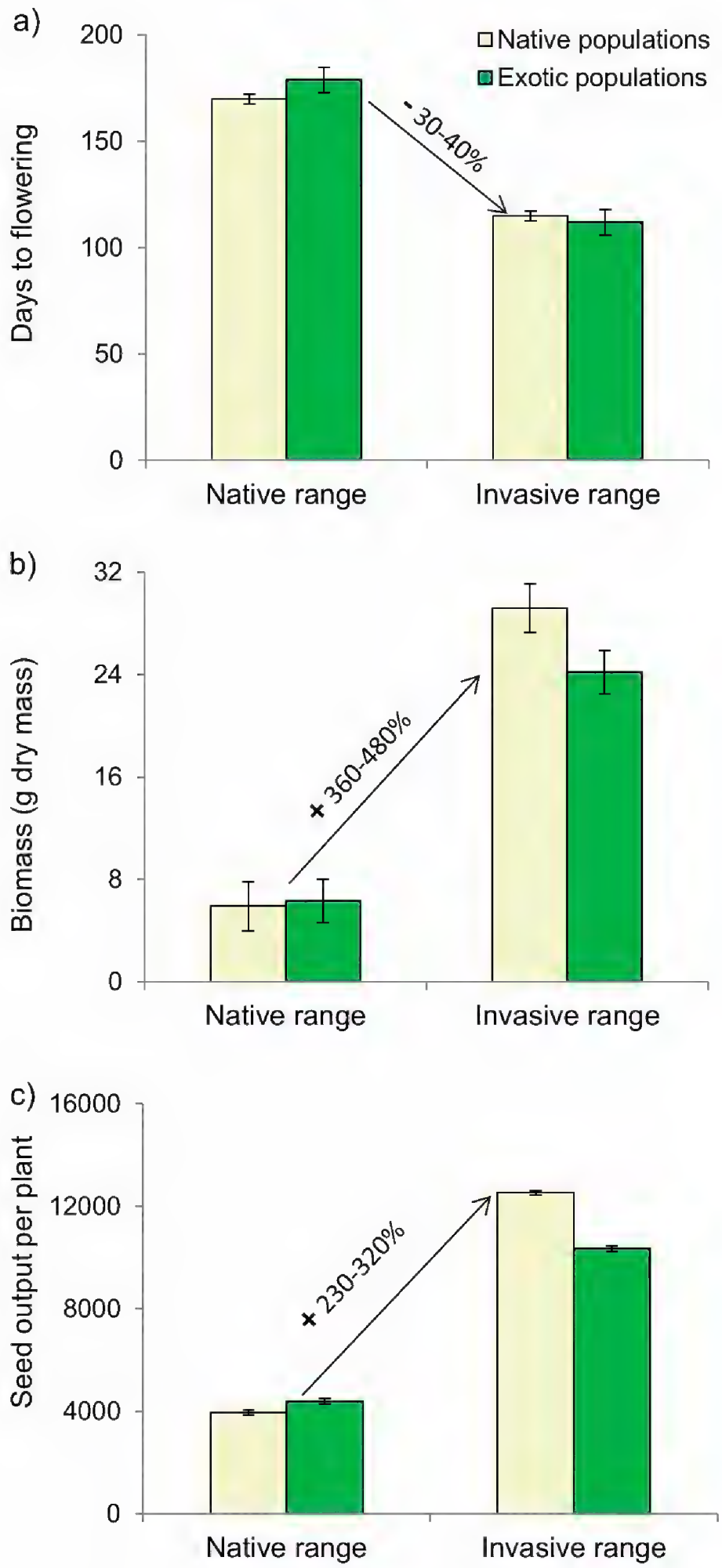

Figure 3. Comparisons between trials at the native and the introduced ranges for native and exotic populations of *Leontodon saxatilis*. Graphs show mean values and standard errors of days to flowering (**a**), biomass per plant (**b**) and seed output per plant (**c**) grouped by origin of the population. Percentages of variation between the native trial and the invasive one are also shown. The arrow indicates the direction of the colonisation process, from the source to the recipient region.

ing range expansion) but it did not increase plant growth (i.e. biomass) nor propagule pressure (i.e. seed output did not result in enhanced days to flowering). Similarly, the delay in *L. saxatilis* phenological development at the native range was not invested in producing more biomass or displaying more seed output, probably due to the lower precipitation at the trial located in the native range compared to the trial at the introduced range. In the case of this species, no consistent patterns were found associated with the country of origin of the populations.

Regarding performance traits, *T. glomeratum* exhibited clear differences in their biomass and seed output displayed associated with the country of origin of the populations. Contrary to what we expected, exotic populations have not apparently undergone selection for traits that allowed them to outperform native populations of the same species; in fact, native populations displayed greater seed output when cultivated under common garden conditions in the introduced range (Table 2). The very same trend was observed for *H. glabra* and *L. saxatilis*. This can be related to the fact that native populations of the three species showed a much lower survival rate than exotic ones under the novel environmental conditions of the introduced range (see Suppl. material 4: Figure S4). Exotic populations of these species might have overcome greater hydric stress typical from the Mediterranean-type region of central Chile by evolving resistance mechanisms, (presumably costly) which in turn trade off against biomass and seed output. Performance traits for *L. saxatilis* were mainly influenced by range (see Martín-Forés et al. 2017c for further discussion); in this sense, the increase in biomass and seed output displayed by *L. saxatilis* in the introduced range compared to the native one, especially highlighted for native populations, reflects the invasive ability of this species, which shows an enhanced propagule pressure in the introduced range and the capacity to spread there. Our findings support the invasion patterns of *L. saxatilis* in central Chile, as it is the most frequent exotic species in this region (Martín-Forés et al. 2012) and it is widely distributed due to its invasiveness (Martín-Forés et al. 2015, 2017c). It is also an invader in other Mediterranean regions such as California and southern Australia (Groves et al. 2003, DiTomaso et al. 2007); thus, such a great plastic response might raise the potential of this species to spread in a global changing scenario (Guerin et al. 2014).

Their particular dispersal pathways could also influence these differences identified amongst species. For instance, *Trifolium glomeratum* has animal-dispersed fruits with low spreading capacity, probably needs to rely more on acclimatising to local conditions and adjusting its phenological development in relation to the precipitation on the origin of the population. On the contrary, both *H. glabra* and *L. saxatilis* have fruit dimorphism (i.e. heterocarpy; Baker and O'Dowd 1982, Brändel 2007); they are not only animal-dispersed but also undergo long distance dispersal events by wind (Martín-Forés et al. 2017c, 2018); in this case, a plastic response in survival, phenology and performance traits could be the most successful mechanism in the novel environment. However, further detailed research would be necessary to elucidate whether different mechanisms operate in the acclimatisation process to a new environment depending of the dispersal pathway of the species.

Conclusion

Overall, the studied invasive species have evolved in their native range for millennia, while in their introduced range, they have only been present for few decades or over the last few centuries. Once they arrived to Chile, they spread and adapted to the whole Chilean climatic gradient. *Trifolium glomeratum* and *H. glabra* mainly relied on ecotypic differentiation for plant phenology associated with the population origin while *L. saxatilis* mainly showed plasticity when growing in different ranges. However, changes in phenology were not reflected in greater biomass or seed output display but might rather be related to range expansion processes. Despite relying on different strategies, all these species have resulted as successful invaders in the Mediterranean Biome. All this highlights that, not only performance traits, but also phenology and plant survival are key traits that need to be targeted to account for species invasiveness and therefore to predict future invasions and control for existing ones.

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Supplementary material 1

Figure S1

Authors: Irene Martín-Forés, Miguel A. Casado, Isabel Castro, Alejandro del Pozo, Marco A. Molina-Montenegro, José M. de Miguel, Belén Acosta-Gallo

Data type: occurrence

Explanation note: Distribution of *Leontodon saxatilis*, *Hypochaeris glabra* and *Trifolium glomeratum* in both the native (Spain) and the introduced (Chile) ranges.

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Link: https://doi.org/10.3897/neobiota.41.29965.suppl1

Supplementary material 2

Figure S2

Authors: Irene Martín-Forés, Miguel A. Casado, Isabel Castro, Alejandro del Pozo, Marco A. Molina-Montenegro, José M. de Miguel, Belén Acosta-Gallo

Data type: occurrence

Explanation note: Map of the studied areas of Mediterranean grasslands in Spain and Chile, including populations sampled following a rainfall gradient (see Table 1). The location of the common gardens is shown (x). This figure has been adapted from Martín-Forés et al. (2015, 2018).

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Supplementary material 3

Figure S3

Authors: Irene Martín-Forés, Miguel A. Casado, Isabel Castro, Alejandro del Pozo, Marco A. Molina-Montenegro, José M. de Miguel, Belén Acosta-Gallo

Data type: species data

Explanation note: Daily maximum and minimum temperatures (A and B) and precipitation (C, D) at Cauquenes, Chile (A, C) and Madrid, Spain (B, D). Data are from 1 January – 31 December 2011 in Chile and 1 July 2011 – 30 June 2012 in Spain. The arrows indicate transplanting dates.

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Supplementary material 4

Figure S4

Authors: Irene Martín-Forés, Miguel A. Casado, Isabel Castro, Alejandro del Pozo, Marco A. Molina-Montenegro, José M. de Miguel, Belén Acosta-Gallo

Data type: statistical data

Explanation note: Tree diagrams for *Leontodon saxatilis*, *Hypochaeris glabra* and *Trifolium glomeratum* showing significant differences in survival curves. Each diagram represents the comparison of Kaplan-Meyer curves considering common garden range (first level: introduced vs native), country of origin (second level: Chile vs Spain), and populations (third level: nomenclature as in Table 1). For each population the percentage of survival is shown and the lowercase letters indicate similar groups amongst populations.

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